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Growth, water relations, and gas exchange of intercropped soybean and velvetleaf

Joan Zaprzalka Cheetham
Iowa State University

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**Growth, water relations, and gas exchange of intercropped
soybean and velvetleaf**

Cheetham, Joan Zaprzalka, Ph.D.

Iowa State University, 1989

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Growth, water relations, and gas exchange of
intercropped soybean and velvetleaf

by

Joan Zaprzalka Cheetham

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GENERAL INTRODUCTION

Velvetleaf (Abutilon theophrasti Medic.) is a major weed of soybean (Glycine max (L.) Merr.) fields and other row crops in the eastern half of the United States (Spencer, 1984). Velvetleaf interferes with soybean growth and causes reductions in seed yield (Dekker and Meggitt, 1983; Eaton et al., 1976; Hagood et al., 1980; Higgins et al., 1983 and 1984; Munger et al., 1987b; Oliver, 1979). Soybean yield losses can be great. Hagood et al. (1980) reported a 26% decrease in soybean seed yield with a velvetleaf density of 2.5 per m² and a 42% decrease in yield with 10 velvetleaf per m². Oliver (1979) reported soybean yield losses of 13 and 27% with velvetleaf densities of 1.6 and 3.2 plants per m², respectively. In addition, the geographic area where velvetleaf is a serious problem appears to be enlarging, and velvetleaf is tolerant to many herbicides used in crop production (Oliver, 1979; Spencer, 1984).

By midseason velvetleaf plants are generally taller than soybeans; velvetleaf then shades the crop canopy as it successfully competes for irradiance (Wax and Stoller, 1985). Competition for water and mineral nutrients may also occur (Donald, 1963; Zimdahl, 1980), and there could be an allelopathic component of velvetleaf interference (Colton and Einhellig, 1980). However, Stoller and Wooley (1985) concluded that, in Illinois, nearly all of the soybean yield loss due to velvetleaf interference could be accounted for by competition for irradiance.

Despite the prevalence of velvetleaf, few studies have addressed the morphological or physiological bases of its competitive success in

soybean fields. Comparative physiological and morphological studies of crops and associated weeds should lead to a better understanding of weed - crop interactions and may allow prediction of competitive success under a range of conditions (Patterson, 1985 and Newman, 1981). In addition, knowledge of the physiology and biology of a weed species should result in more efficacious control and could possibly serve as a basis for the selection of more competitive and productive crop varieties (Radosevich and Holt, 1984; Patterson, 1982).

In the present study we investigated the competitive strategy of velvetleaf in soybean in terms of physiological and morphological parameters. In part one we attempted to determine if leaf physiological processes could be contributing to velvetleaf interference ability in soybean. We compared, under field conditions, leaf water relations and gas exchange characteristics of intercropped soybean and velvetleaf plants. A secondary objective was to determine if velvetleaf in soybean influences soybean water relations and gas exchange. In part two of the study our objective was to investigate the role of plant morphological and growth parameters in velvetleaf competitive success in soybean. To achieve this objective we monitored selected aboveground growth characteristics of intercropped soybean and velvetleaf plants throughout the growing season.

Explanation of Dissertation Format

This dissertation was prepared under the alternate format option at Iowa State University. The two research papers forming the main body of the work are intended for submission to the journal Weed Science. For each of these papers the senior author designed and completed the necessary field experiments and also statistically analyzed and interpreted the data presented.

GENERAL LITERATURE REVIEW

Water Relations and Gas Exchange of Crops
and Associated Weeds

Relatively few field studies have compared water relations and gas exchange characteristics of crop species and their associated weeds. Such studies should reveal a possible plant physiological basis for competitive success in an agroecosystem. In Texas, Stuart et al. (1984) compared the field water relations of cotton (Gossypium hirsutum L.) and smooth pigweed (Amaranthus hybridus L.). Pigweed maintained higher leaf water potentials and turgor pressure than cotton as a result of water extraction at lower soil depths and lower stomatal conductance. The authors concluded that smooth pigweed successfully competes with cotton for water. Scott and Geddes (1979) investigated the effects of field water stress on intercropped soybean and common cocklebur (Xanthium pensylvanicum Wallr.). During vegetative growth cocklebur had lower midday leaf water potentials, while during reproductive growth soybean leaf water potentials were lower. Also, throughout the growing season stomatal conductance values for soybean were generally lower than those of cocklebur. It appeared that soybeans were under greater stress than cocklebur during the critical reproductive period. In another study, Geddes et al. (1979) found that the roots of common cocklebur explored a greater volume of soil than did soybean; this was also found to be true for tall morningglory in soybean (Scott and Oliver, 1976). Greater root development may partially account for the competitive success of these 2

weeds in soybean, especially during droughty periods late in the season. Cruz et al. (1983) reported that 3 common weeds of dryland rice (Oryza sativa L.) were able to maintain higher midday and predawn leaf water potentials than rice. They hypothesized that the weeds had greater root system development than rice.

Several researchers have compared water relations and gas exchange parameters of velvetleaf and soybean or cotton under controlled environment conditions, however the relevance of these studies to field situations is not known. Regnier et al. (1988) reported that field-grown soybean and velvetleaf plants had similar maximum leaf photosynthetic rates when the rates were measured under laboratory conditions. Patterson and Flint (1983) found no differences in leaf photosynthetic rates between vegetative soybean and velvetleaf plants, even though soybean stomatal conductance was higher. They did find interspecific differences in stomatal response to decreasing leaf water potential. Soybean stomatal closure began at -1.0 MPa, while velvetleaf stomatal closure began at about -1.3 MPa. Munger et al. (1987a) also examined the effects of water stress on soybean and velvetleaf. Velvetleaf stomatal conductance, net photosynthetic rates and transpiration rates were consistently higher than those of soybean for leaf water potentials ranging from -0.7 to -2.7 MPa. In addition, the relationship between photosynthetic rate and stomatal conductance was different for soybean and velvetleaf. At similar levels of stomatal conductance, velvetleaf photosynthetic rates were generally higher than those of soybean. Patterson (1988) found no differences in stomatal

conductance, leaf transpiration rate or leaf water potential between well-watered cotton and velvetleaf plants. Under water stress, however, leaf water potential tended to be lower in cotton. These studies indicate that interspecific differences in water relations and gas exchange parameters could influence competitive relationships between crops and weeds, especially under conditions of limited soil moisture.

Weed Interference with Crop Water Relations and Gas Exchange

Some recent research has focused on the effects of weeds on crop water relations in order to determine if interspecific competition for water is occurring. In a field study in Texas Munger et al. (1987b) found no differences in leaf water potential between monocultured soybeans or those intercropped with velvetleaf at 5 plants per m². They concluded that little or no competition for water was occurring. The authors also reported that soybeans at the R6 stage (Fehr et al., 1971) extracted water from deeper in the soil profile than velvetleaf, however, plant density was a confounding factor in their study. These same researchers reported no differences in photosynthetic rates or stomatal conductance between monocultured or intercropped soybeans in a moist year. However, in a dry year, differences did exist during early reproductive stages of soybeans. Midafternoon photosynthetic rates and stomatal conductance were lower in intercropped soybeans, while leaf temperatures were higher.

Stuart et al. (1984) examined the response of cotton water relations to smooth pigweed competition under field conditions. The presence of pigweed reduced cotton water potential early in the season (but there was no effect on cotton diffusive resistance) and increased it later in the season probably as a result of shading. Pigweed competition reduced soil water content relative to cotton alone. Cruz et al. (1983) reported that weeds of dryland rice caused a decline in rice leaf water potential and leaf length. They concluded that competition for soil water was occurring. Thus, it appears that certain weed species can have a negative influence on crop water relations by successfully competing for soil moisture reserves.

Growth of Crops and Associated Weeds

Mathematical growth analysis is a valuable technique for determining how environmental factors influence plant dry matter production and resource allocation and therefore can be used to study interference between species in the agroecosystem (Sestak, Catsky, and Jarvis, 1971). Relatively few investigators have evaluated crop and associated weed growth analysis characteristics under field conditions. After 10 weeks of growth, intercropped velvetleaf plants (at 5 plants per m²) were taller and had more main stem nodes and greater dry weight than soybean plants (Munger et al., 1987b). Regnier et al. (1988) reported that 3 to 4 week old field-grown (in containers) soybean and velvetleaf plants showed no differences in net assimilation rate, relative growth rate, or specific leaf area. However, leaf area ratio

and leaf weight ratio were greater for velvetleaf. Field studies indicated that johnsongrass (Sorghum halepense (L.) Pers.) outcompeted cotton (Gossypium hirsutum L.), yellow nutsedge (Cyperus esculentus L.) and purple nutsedge (Cyperus rotundus L.) (Holt, 1986; Holt and Orcutt 1987). The authors concluded that parameters affecting interception of irradiance (height, leaf area, specific leaf area, and canopy density) were good indicators of competitive success in these 4 species. Thus, competition for irradiance may be more important here than competition for water or nutrients or other types of interference.

The competitive nature of common cocklebur (Xanthium strumarium L.) in soybean was attributed to rapid early growth and root elongation rate, while tall morningglory (Ipomoea purpurea (L.) Roth.) was successful due to a rapid shoot elongation rate (Monks et al., 1988). Geddes et al. (1979) reported that intercropped cocklebur produced dry matter 3 times greater than that of soybean. Oliver et al. (1976) concluded that soybeans were more competitive than tall morningglory for the first 6 to 8 weeks after emergence. The competitive success of tall morningglory in soybean was dependent on a rapid increase in leaf area which occurred 4 to 6 weeks after emergence. Additional field studies comparing growth parameters of crops and associated weeds should result in a better understanding of competitive relationships and mechanisms in cropping situations.

Several investigators have evaluated weed versus crop growth characteristics under greenhouse and growth chamber conditions, but the relevance of these results to field conditions is not known. During the

first 5 weeks of growth, velvetleaf and cotton were judged to be approximately equal in competitive ability (Elmore et al., 1983). This conclusion was based on plant height, leaf area, plant dry weight, and mean relative yields in mixtures. In other studies, velvetleaf dry matter production, relative growth rate (RGR), relative leaf area expansion rate (LAER), net assimilation rate (NAR), leaf area duration (LAD), and leaf area partitioning (LAP) were greater than those of cotton during early growth of both species (Patterson et al., 1978; Patterson and Flint, 1979; Patterson, 1988). These results indicate that velvetleaf plants could eventually outgrow the initially larger cotton plants. Under water stress cotton dry matter production, NAR, and LAD were reduced less than those of velvetleaf, suggesting that drought conditions during vegetative growth may increase cotton competitiveness relative to velvetleaf (Patterson, 1988).

In growth chamber experiments RGR, LAER, and relative leaf weight growth rate of 1 to 4 week old velvetleaf were consistently higher than those of soybean and the differences were greater under warmer temperature regimes (Potter and Jones, 1977). Another study reported that 4 week old velvetleaf had less leaf area and less plant total dry weight than soybean (Patterson and Flint, 1983). In addition, velvetleaf allocated less dry matter to stem and more to leaf weight and area than soybean. Velvetleaf plants also had slightly higher net assimilation rates (NAR), while leaf area duration (LAD) was greater for soybean. Thus a rapid early growth rate may allow velvetleaf in soybean or cotton to overcome an initial deficit in leaf area, height, and total

dry weight. Whether this occurs under field conditions remains to be demonstrated. According to Grime (1979) weeds of arable land generally have rapid early growth rates. In addition, Grime and Hunt (1975) concluded that in natural habitats a high relative growth rate is one of a number of traits that characterize a competitive species.

Weed Interference with Soybean Growth and Development

Several investigators have monitored the effects of weeds on soybean growth parameters during the growing season. Such research indicates the timing and nature of weed interference effects on crop growth and development. Munger et al. (1987b) reported that intercropped velvetleaf (at 5 plants per m²) reduced soybean height, leaf area index (LAI), number of main stem nodes, total number of leaves, and plant aboveground dry weight. The reductions were detected 10 to 12 weeks after crop emergence and were more severe in the drier than normal growing season. Hagood et al. (1980) reported that by approximately 75 days after emergence velvetleaf at 2.5 and 5.0 plants per m² had reduced soybean LAI and leaf, stem, pod, and total plant dry weights. Soybean leaf weight and area appeared most sensitive to velvetleaf interference. In Arkansas, velvetleaf at 1.6 and 3.2 per m² reduced soybean LAI. Soybean crop growth rate (CGR) was also decreased by the higher weed density, and soybean plants showed the effects of interference earlier in the season. Velvetleaf was not competitive in late planted soybeans due to early floral initiation and consequent slowing of leaf growth (Oliver, 1979). In Kansas, velvetleaf dry matter

was greatly reduced when planting was delayed for 10 days after soybean planting and effects on soybean yields were much less than when planted at the same time as soybean (Eaton et al., 1976). Velvetleaf planted 20 or more days after soybeans was greatly reduced in height and did not affect soybean yield. Dekker and Meggitt (1983) reported reductions in soybean dry matter, number of branching and flowering nodes, and seed yield due to the presence of velvetleaf at 2.4 and 3.7 plants per m². They also reported no interspecific differences in leaf mineral nutrient content at midseason, and therefore concluded that competition for soil nutrients played little or no role in soybean - velvetleaf interference. In Iowa, velvetleaf densities of 0.4 and 0.9 per m² caused changes in nearby soybean plants (Higgins et al. 1983 and 1984). Soybeans adjacent to weed plants had smaller leaf areas, fewer main stem nodes, and reduced leaf, stem and total dry weights. Reductions in soybean crop growth rate and relative growth rate were also evident.

Oliver et al. (1976) reported that interference by tall morningglory at 1.6 and 6.5 plants per m² reduced soybean LAI, plant dry weight, and CGR. Soybean leaf and stem dry weight were equally affected, and the effects of tall morningglory were first evident 6 to 8 weeks after emergence. No differences in soybean leaf to stem ratio (LTSR), height, NAR or RGR were found due to weed interference. Cordes and Bauman (1984) found that the best indicators of ivyleaf morningglory (Ipomoea hederacea (L.) Jacq.) interference were reductions in soybean LAI, plant dry weight, and seed yield. No effects on soybean plant height or CGR were seen, and no interference effects were detectable

before soybeans began reproductive growth. Bloomberg et al. (1982) reported that the main response to common cocklebur (Xanthium pensylvanicum Wallr.) interference was a decrease in soybean seed yield in years when rainfall was close to normal, but when water was limited soybean vegetative growth was affected more than yield. Geddes et al. (1979) found that soybean dry matter and LAI were decreased by common cocklebur competition beginning about 8 weeks after emergence, and the reductions were greater during the drier than average growing season. They concluded that a primary effect of interspecific competition was a reduction in leaf expansion. Barrentine and Oliver (1977) reported that reductions in soybean LAI, dry matter, and CGR were good indicators of when common cocklebur began to compete with soybean.

SECTION I. WATER RELATIONS AND GAS EXCHANGE OF
INTERCROPPED SOYBEAN AND VELVETLEAF

Water Relations and Gas Exchange of Intercropped Soybean (Glycine max)
and Velvetleaf (Abutilon theophrasti)

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ABSTRACT

Water relations and gas exchange characteristics of intercropped soybean and velvetleaf plants were compared during 1985 and 1986 in a field study at Ames, Iowa. Throughout the growing season, velvetleaf predawn and midday leaf water potentials were consistently lower than those of soybean. Midday stomatal conductances, midday leaf transpiration rates, and daily mean photosynthetic rates were higher for velvetleaf during the vegetative growth stage of both species, but thereafter were higher for soybean. Soybean and velvetleaf plants differed in the relationship between midday stomatal conductance and leaf water potential. Despite lower leaf water potentials, velvetleaf was able to maintain stomatal conductances comparable to or greater than those of soybean from early to midseason. Low leaf water potentials could enhance velvetleaf competitiveness in soybean by increasing efficiency of soil water extraction. Soybean and velvetleaf showed a similar relationship between leaf photosynthetic rates and stomatal conductance, indicating no interspecific differences in photosynthetic efficiency. In the drier than average year (1985), soybeans intercropped with velvetleaf had slightly lower predawn leaf water potentials in comparison to monocultured soybeans. No differences in midday leaf water potentials, stomatal conductances, or photosynthetic rates were detected between monocultured and intercropped soybean.

Nomenclature: soybean, Glycine max L. Merr. 'Corsoy 79'; velvetleaf, Abutilon theophrasti Medic.

Additional index words. Leaf water potential, stomatal conductance, photosynthesis, competition.

INTRODUCTION

Velvetleaf is a major weed of soybean fields and other row crops in the eastern half of the United States (Spencer, 1984). Velvetleaf interferes with soybean growth and causes reductions in seed yield (Hagood, 1980; Oliver, 1979; Higgins, 1984). By overtopping the soybean canopy velvetleaf successfully competes for irradiance (Stoller and Woolley, 1985). Competition for water and mineral nutrients may also occur (Zimdahl, 1980), and there may be an allelopathic component of velvetleaf interference (Colton and Einhellig, 1980). Despite the prevalence of velvetleaf, little information is currently available concerning a possible physiological basis for its competitive success in soybean.

Comparative physiological studies of crops and associated weeds should lead to a better understanding of weed - crop interference (Patterson, 1985). Several studies have compared soybean and velvetleaf physiological parameters under controlled environment conditions, but extrapolation of these results to field conditions is difficult. From laboratory measurements Regnier et al. (1988) determined that field-grown soybean and velvetleaf plants had similar light response curves and maximal rates of leaf photosynthesis. Dark respiration rates and leaf thickness were also similar for the 2 species. Patterson and Flint (1983) found no differences in leaf photosynthetic rates between vegetative soybean and velvetleaf plants, even though soybean stomatal conductances were higher. They did report differences in stomatal

response to decreasing water potential, with soybean stomatal closure beginning at higher leaf water potential values. During reproductive growth, velvetleaf stomatal conductance and leaf photosynthetic rates were reported to be consistently higher than those of soybean over a range of leaf water potential values (Munger et al., 1987a). In addition, interspecific differences were found in the relationship between photosynthetic rate and stomatal conductance. At similar levels of stomatal conductance, velvetleaf generally had higher photosynthetic rates than soybean. Patterson (1988) found no differences in stomatal conductance, leaf transpiration rate or leaf water potential between well-watered cotton and velvetleaf plants. Under water stress, however, leaf water potential tended to be lower in cotton.

A few field studies have examined weed versus crop physiological characteristics. In Texas, soybean leaf water potentials were generally higher than those of velvetleaf during the reproductive growth stages of both species (Munger et al., 1987b). There appeared to be no interspecific differences in midday photosynthetic rates, while stomatal conductance was generally higher in soybean. Stuart et al. (1984) reported that smooth pigweed (Amaranthus hybridus L.) maintained higher leaf water potentials and turgor pressure than cotton (Gossypium hirsutum L.), probably as a result of greater soil water extraction and lower stomatal conductance. The authors concluded that smooth pigweed successfully competes with cotton for water. Scott and Geddes (1979) compared the field water relations of soybean and common cocklebur (Xanthium pensylvanicum Wallr.). During vegetative growth cocklebur had

lower midday leaf water potentials, while later in the season soybean readings were lower. In addition, soybean stomatal conductances were generally lower than those of cocklebur. Soybeans appeared to be under greater stress than cocklebur during the critical reproductive period. In another study, it was found that the roots of common cocklebur explored a greater volume of soil than did soybean (Geddes et al., 1979). Greater root development may partially account for the more favorable water relations status of cocklebur in comparison to soybean.

Related research has focused on the effects of weeds on crop water relations in order to determine if interspecific competition for water occurs under field conditions. No differences in leaf water potential, stomatal conductance or transpiration rate were detected between monocultured soybeans or those intercropped with velvetleaf (Munger et al., 1987b). The authors concluded that little or no competition for water was occurring, and they also reported that soybeans appear to extract water from deeper in the soil profile than velvetleaf; however, plant density was a confounding factor in their study. Intercropped pigweed reduced cotton water potential early in the season (there was no effect on cotton stomatal conductance) and increased it later in the season, probably as a result of shading (Stuart et al., 1984). Pigweed competition also reduced soil water content relative to cotton alone.

In the present study, our primary objective was to determine if velvetleaf competitive success in soybean can be at least partially attributed to physiological characteristics. The specific objectives were a) to determine whether interspecific differences in gas exchange

and water relations parameters exist between intercropped soybean and velvetleaf plants under field conditions, and b) to determine if intercropped velvetleaf have an effect on soybean water relations and gas exchange parameters.

MATERIALS AND METHODS

Field plot establishment. A 2 year field study on the Curtiss Research Farm at Ames, IA examined leaf physiological parameters of velvetleaf and soybean plants. In 1985 the plots were located on a Nicollet loam soil (fine-loamy, mixed, mesic Aquic Hapludolls), and in 1986 the plots were established on Clarion loam (fine-loamy, mixed, mesic Typic Hapludolls). Standard midwestern fertilizer and seeding practices were used to plant soybeans. Treatments consisted of monocultured soybeans (at 35/m²) and soybeans (at 35/m²) intercropped with velvetleaf at 0.5, 1.0 and 2.0 per m². These levels were chosen to simulate conditions where velvetleaf control methods have been only partially effective. Experimental design was a randomized complete block with 4 replications of each treatment in 1985 and 6 in 1986. Velvetleaf seeds were hand planted approximately 10 cm from the soybean row and spaced along the row. Soybeans were seeded on May 15 in 1985 and on May 22 in 1986, while velvetleaf were seeded on May 16 in 1985 and May 22 in 1986. Both species were overseeded and then thinned to the desired densities after emergence. Emergence for both species was May 23 in 1985 and May 29 in 1986. Plot size was 6 rows (0.76 m apart) by 9.8 m in 1985 and 10.4 m in 1986. Sethoxydim (2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one) at 0.2 kg active ingredient/ha (1986 only) and handweeding were used to control weeds. Rainfall data were gathered onsite and at a National Weather Service station 9.6 km to the west.

Physiological measurements. For both species biweekly physiological measurements were begun at about 5 weeks after emergence, at soybean V6 stage (Fehr et al., 1971) in late June, and continued through approximately 13 weeks after emergence in late August (soybean R6). All measurements for both species were obtained from the youngest fully developed leaf in full sun at canopy top. Within each plot adjacent velvetleaf and soybean plants were sampled. Subsamples within a plot consisted of 1 to 3 leaves of each species.

Leaf water potential was measured at predawn and midday with a portable pressure chamber¹. Predawn measurements were taken between 0600 and 0700 h CDT, while midday readings were taken between 1200 and 1500 h CDT. A steady state porometer² was used to measure stomatal conductance and leaf transpiration rates. Readings from upper and lower leaf surfaces were added to give a total value. Midday readings were taken between 1200 and 1500 h CDT. In addition, in 1985 diurnal porometer readings were taken every 2 h beginning at 0900 h and ending at 1700 h CDT for 2 replicates each of the monoculture and the 2.0 velvetleaf per m² treatments. In 1986 the leaves used for porometer readings were immediately excised and then used for the pressure chamber readings. In 1985 different leaves were used for porometer and pressure chamber readings. Net photosynthetic rates, as well as stomatal conductance and transpiration rates, were obtained with a portable

¹ Model 3005, Soilmoisture Equipment Corp., Santa Barbara, CA.

² Model LI-1600, Li-Cor Inc., Lincoln, NE.

photosynthesis system³. In 1985, measurements were taken between 1100 and 1300 h CDT on July 22 and August 18. In 1986 biweekly, diurnal readings were taken beginning at 0900 h and ending at 1700 h CDT. Only 3 replications were used for the 1986 photosynthesis measurements.

Statistical analyses. Data were subjected to regression analysis and analysis of variance. For species comparisons the monoculture treatment was deleted. Subsequent analyses revealed no significant treatment effects, so the means presented for the species comparisons are the averages over the 3 velvetleaf density treatments. When the F values were significant (0.05 level), least significant differences (0.05 level) were computed to determine significant differences among mean values.

³ Model LI-6000, Li-Cor Inc., Lincoln, NE.

RESULTS AND DISCUSSION

Precipitation. The 1985 and 1986 growing seasons differed in terms of rainfall pattern. Precipitation was well below the 30 year average in 1985 through midseason, while in 1986 rainfall was above average for every month from April through September (Table 1). The severity of weed interference in agronomic crops can be influenced by seasonal precipitation patterns (Geddes et al., 1979; Hagood et al., 1980). In midwestern soybean fields weed interference is generally most intense when precipitation is adequate through midseason and limited thereafter (Staniforth, 1958; Eaton et al., 1973).

Plant water status. Velvetleaf predawn leaf water potentials were consistently lower than those of adjacent soybean plants (Figure 1). The differences were statistically significant for all dates of measurement in 1986 and for all but the second date in 1985. Velvetleaf midday leaf water potentials were significantly lower than those of adjacent soybean at all dates of measurement for both years (Figure 2). These findings are consistent with limited field data reported previously (Munger et al., 1987a).

Lower water potentials generally indicate a greater degree of plant water stress, but the relationship varies among species due to physiological factors such as osmotic adjustment (Hsiao, 1973). From leaf water potential data alone it is not possible to conclude that velvetleaf is under more water stress than soybean. Turgor potentials

were not measured in this study. Other studies have revealed that invading weeds are often able to maintain higher leaf water potentials than the crop. This was reported for smooth pigweed in cotton (Stuart et al., 1984), rice (*Oryza sativa* L.) and three associated weeds (Cruz et al., 1983), and for common cocklebur in soybean during reproductive growth (Scott and Geddes, 1979). It was concluded that these weeds were successfully competing with the crop for soil moisture reserves. In contrast, several previous studies have indicated that competition for water may not be an important component of velvetleaf - soybean interference (Munger et al., 1987b; Stoller and Woolley, 1985).

Interspecific differences were also present in the daily and seasonal ranges of leaf water potential values. Velvetleaf had a greater seasonal range of predawn water potential than soybean during both growing seasons (Figure 1). In addition, for all dates of measurement, the diurnal range of water potential was greater for velvetleaf than for soybean (Figures 1 and 2). The seasonal means indicate an average difference between predawn and midday water potentials of 0.4 and 0.3 MPa for soybean and 1.0 and 0.8 MPa for velvetleaf in 1985 and 1986, respectively. Munger et al. (1987a) also reported a greater diurnal fluctuation in water potential for velvetleaf in comparison to soybean during early reproductive growth.

Stomatal conductance and photosynthesis. Velvetleaf midday stomatal conductance was significantly greater than that of adjacent soybean plants at the first date of measurement for both years (Figure 3). This

corresponded to the vegetative growth period for both species. Velvetleaf was able to maintain higher stomatal conductance than soybean early in the season despite having, at the same time, significantly lower midday leaf water potential values. Diurnal measurements taken 39 and 36 days after emergence in 1985 and 1986, respectively, indicated that the higher stomatal conductance for velvetleaf was maintained throughout the day (data not shown). From mid-July through the end of August (approximately 50 to 95 days after emergence) velvetleaf stomatal conductance was lower than that of adjacent soybean plants, although the differences were not statistically significant at the second and third dates of measurement in 1985. Interspecific differences in leaf transpiration rate followed the same seasonal pattern as stomatal conductance in both 1985 and 1986 (data not shown).

The stomatal conductance and leaf water potential data indicate that velvetleaf may be more tolerant of limited soil moisture than soybean. For both species, mean seasonal midday leaf water potentials were about 20% lower in 1985 (the drier than normal season) in comparison to 1986. At the same time however, mean seasonal midday stomatal conductance was about 40% lower for soybean and only about 20% lower for velvetleaf in 1985 as compared to 1986.

In 1986, mean daily photosynthetic rates were measured on 4 dates. Seasonal interspecific differences were similar to those found for stomatal conductance (Figure 4). Early in the season velvetleaf leaf photosynthetic rates were significantly greater than those of adjacent soybean plants. By mid-July (50 days after emergence), however, soybean

leaves had higher photosynthetic rates and this remained true for the rest of the season. Midday photosynthetic rates were measured on 2 dates during reproductive growth in 1985 (60 and 87 days after emergence). The rates were similar to those obtained in 1986, however, although soybean had the higher rate of gas exchange on both dates, the interspecific differences were not significant (see Appendix Table 5).

The higher gas exchange capacity of velvetleaf early in the growing season may give this species a growth rate advantage over soybean during vegetative growth. In both years of this study velvetleaf plants were initially shorter and had less leaf area and plant dry weight than soybean. However, a rapid rate of growth allowed velvetleaf to reverse this growth differential by midseason (Cheetham and Taylor, 1989).

Relationship of stomatal conductance and transpiration rate to leaf water potential. In both 1985 and 1986 adjacent soybean and velvetleaf plants differed in the relationship between midday stomatal conductance and leaf water potential (Figure 5). Despite consistently lower leaf water potentials, velvetleaf plants were able to maintain a seasonal range of stomatal conductances generally comparable to those of soybean. Thus, lower leaf water potentials did not indicate that velvetleaf was under more water stress than soybean. In addition, regression analyses indicated a significant relationship between stomatal conductance and water potential for soybean but not for velvetleaf. For velvetleaf, stomatal conductance appears less dependent on leaf water potential, at least under the field conditions encountered in this study. Munger et

al. (1987a) also reported that, under greenhouse conditions, velvetleaf maintained stomatal conductances similar to those of soybean while its leaf water potential values were lower. However, they reported a significant relationship between velvetleaf stomatal conductance and leaf water potential, but this was after only 1 drying cycle and therefore is not comparable to field conditions.

The lower leaf water potentials of velvetleaf would result in a steeper gradient between plant and soil water potentials. This would allow velvetleaf to extract soil water down to lower matric potentials and therefore should increase both the amount of soil water available to this species and also the period of time over which water is available (Fitter and Hay, 1987). As a result, velvetleaf competitiveness in soybean may be enhanced. Velvetleaf may undergo osmotic adjustment in order to maintain cell turgor and keep stomata open at low leaf water potentials. No data are currently available on velvetleaf capacity for osmotic adjustment. Soybeans appear to have little capacity for osmotic adjustment (Turner et al., 1978).

Interspecific differences in the relationship between transpiration rate and leaf water potential were similar to those seen for stomatal conductance and water potential (Figure 6). Again, the relationship was stronger for soybean than for velvetleaf.

Relationship between photosynthesis and stomatal conductance.

Regression analyses indicated no interspecific differences in the relationship between leaf photosynthetic rate and stomatal conductance

(Figure 7). Since it appears likely that stomata regulate CO₂ diffusion to match the photosynthetic capacity of the leaf mesophyll cells (Nobel, 1983), the data indicate that fieldgrown soybean and velvetleaf plants do not differ in photosynthetic efficiency. In contrast, a recent greenhouse study reported that at similar stomatal conductances photosynthetic rates were generally higher for velvetleaf than for soybean (Munger et al., 1987a). That does not appear to be true under the midwest field conditions of this study.

Effects of velvetleaf interference on soybean water relations. In 1985 intercropped velvetleaf had a small but significant effect on adjacent soybean plant water status. At the second date of measurement in mid-July (soybean R2) soybean predawn leaf water potential decreased from -0.11 MPa in the monoculture treatment to -0.18 and -0.15 MPa for soybean intercropped with velvetleaf at 1 and 2 plants per m², respectively (LSD_{0.05} = 0.03). Monocultured soybean continued to have higher water potentials for the remainder of the season, but the differences were nonsignificant. Seasonal mean predawn leaf water potentials were -0.07 MPa for monocultured soybean and -0.09 MPa for soybean intercropped with velvetleaf at 1 and 2 plants per m² (LSD_{0.05} = 0.018). In 1986 no differences in water potential were found between monocultured soybean and those intercropped with velvetleaf. Precipitation was above average throughout the 1986 growing season (Table 1) so it is not surprising that no water potential differences were detected. The data indicate

that, in drier than normal years, velvetleaf can influence soybean water relations and therefore competition for water may be occurring.

It is not known if such relatively small differences in leaf water potential due to velvetleaf interference could affect soybean seed yield. In Texas, Munger et al. (1987b) concluded that competition for water played no role in soybean yield reduction due to velvetleaf interference, and, in Illinois, Stoller and Woolley (1985) attributed most of the decreased soybean yield due to velvetleaf interference to competition for irradiance. No differences in midday leaf water potentials, midday stomatal conductance, or photosynthetic rates were detected between monocultured and intercropped soybean for either year. A larger experiment may be necessary to detect physiological differences at midday due to large differences in microclimate.

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Table 1. Monthly precipitation for the 1985 and 1986 growing seasons and the 30 year average precipitation at Ames, Iowa.

Month	Precipitation		
	1985	1986	30 year average
	----- (cm) -----		
April	3.1	13.2	8.6
May	3.2	13.8	11.1
June	6.1	16.9	13.0
July	5.2	11.5	8.8
August	15.8	11.2	9.9
September	10.2	17.5	8.2
Total	43.6	84.1	59.6

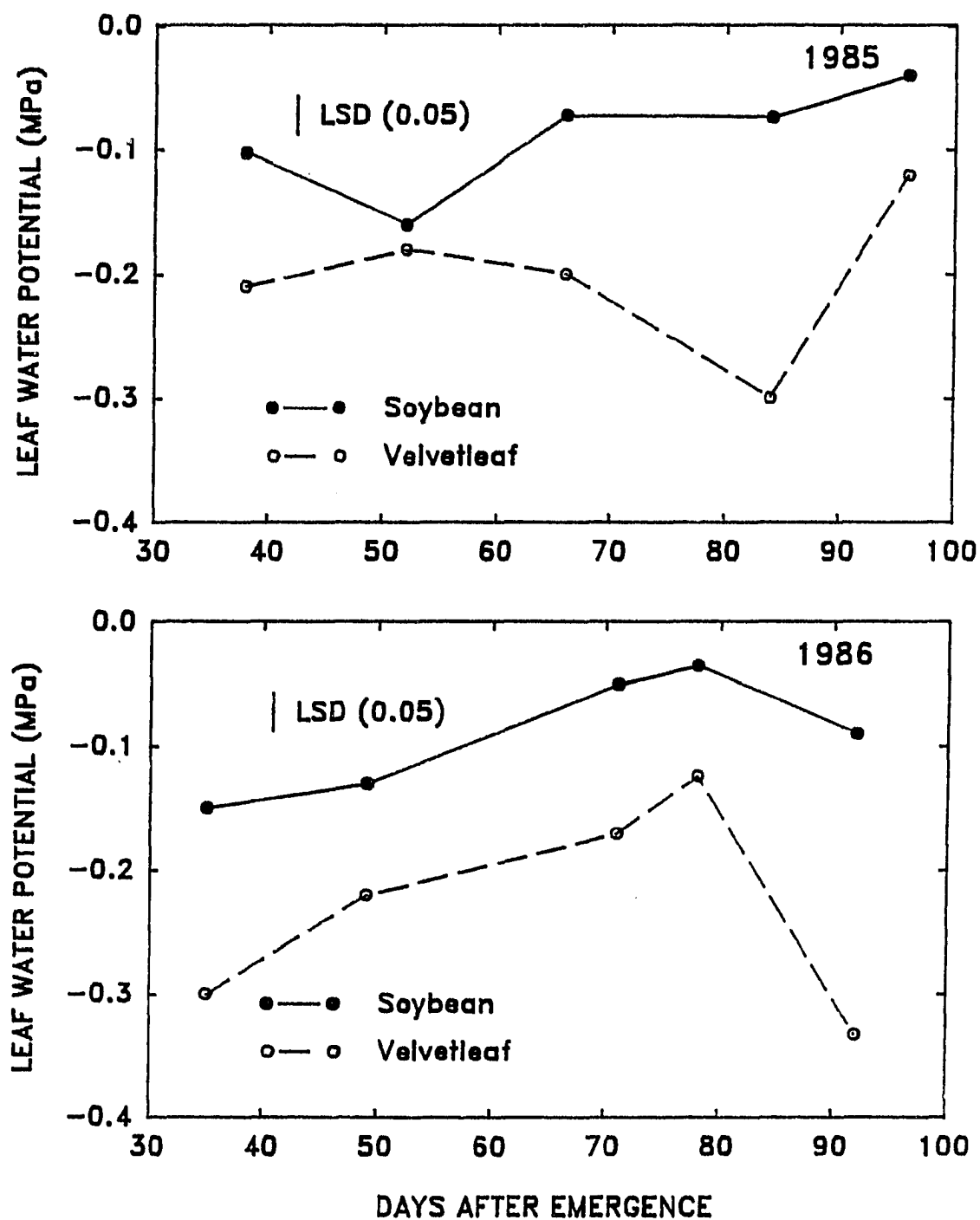


Figure 1. Predawn leaf water potentials of intercropped velvetleaf and soybean on 5 dates in 1985 and 1986 at Ames, IA. LSD values apply to both intra- and interspecific mean comparisons.

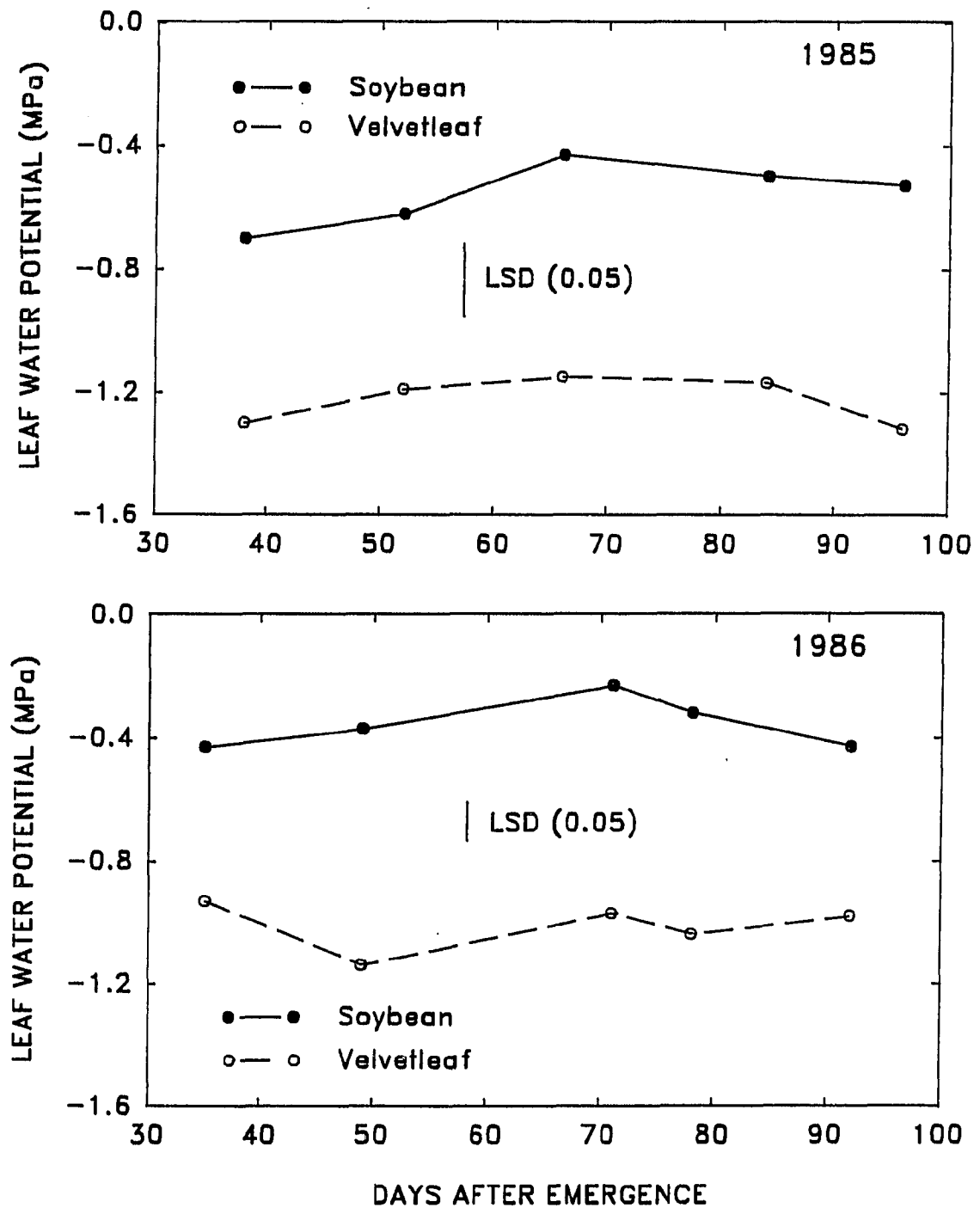


Figure 2. Midday leaf water potentials of intercropped velvetleaf and soybean on 5 dates in 1985 and 1986 at Ames, IA. LSD values apply to both intra- and interspecific mean comparisons.

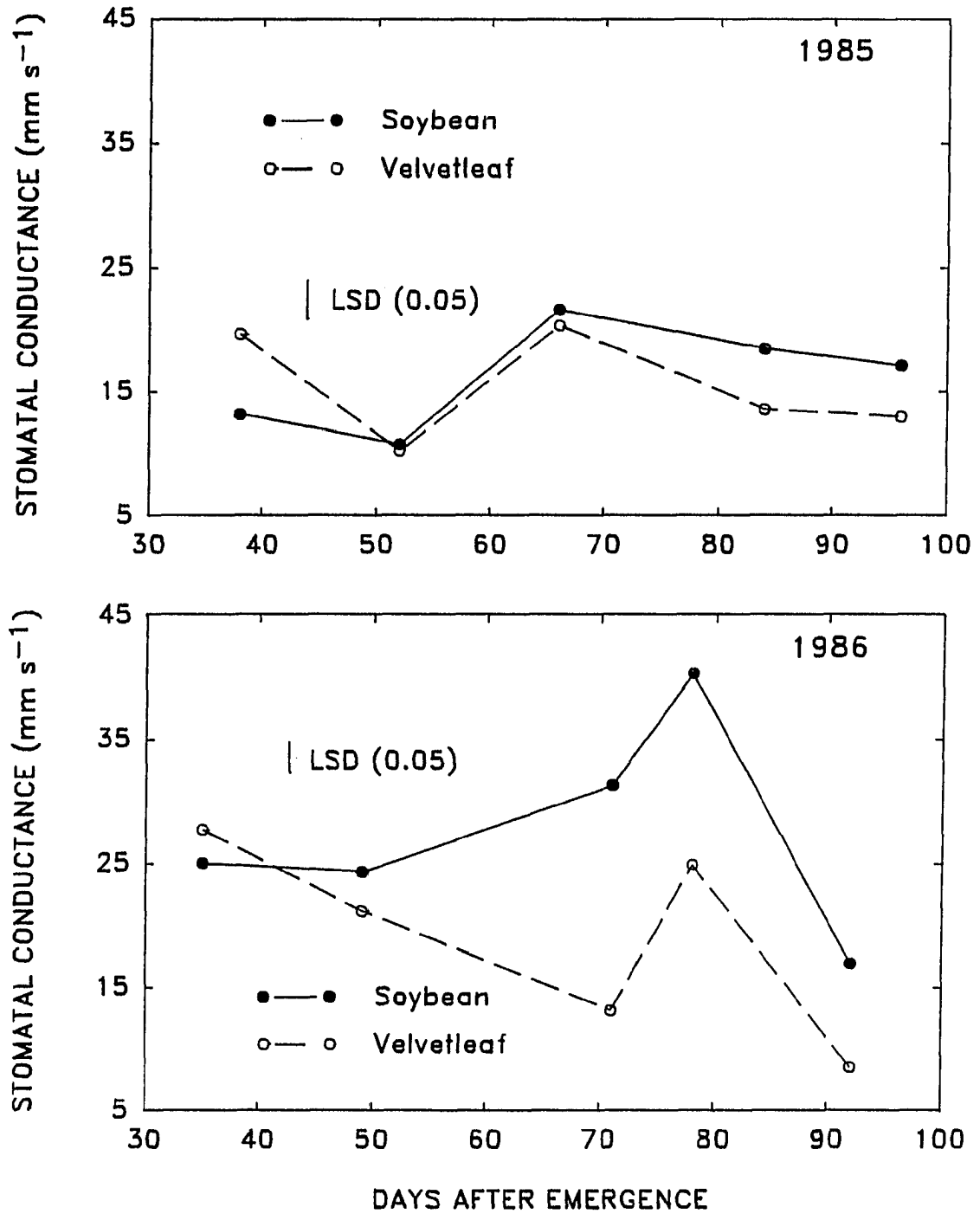


Figure 3. Midday stomatal conductances of intercropped velvetleaf and soybean on 5 dates in 1985 and 1986 at Ames, IA. LSD values apply to both intra- and interspecific mean comparisons.

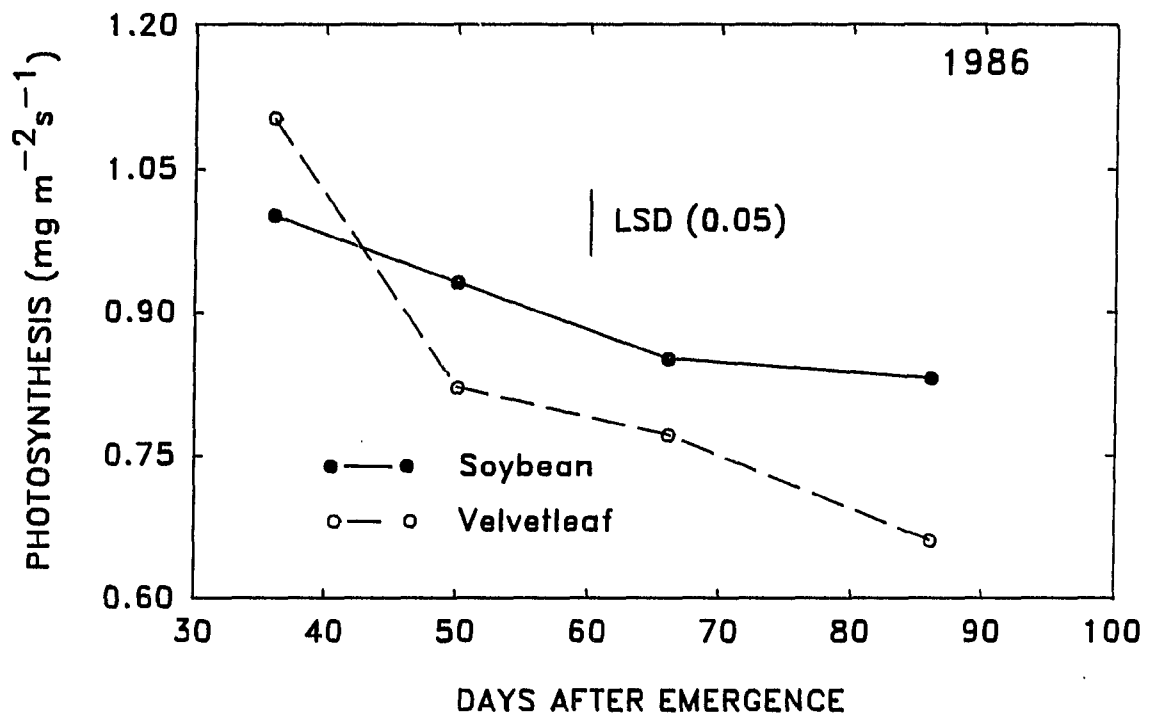


Figure 4. Net photosynthetic rates of intercropped velvetleaf and soybean on 4 dates in 1986 at Ames, IA. LSD values apply to both intra- and interspecific mean comparisons.

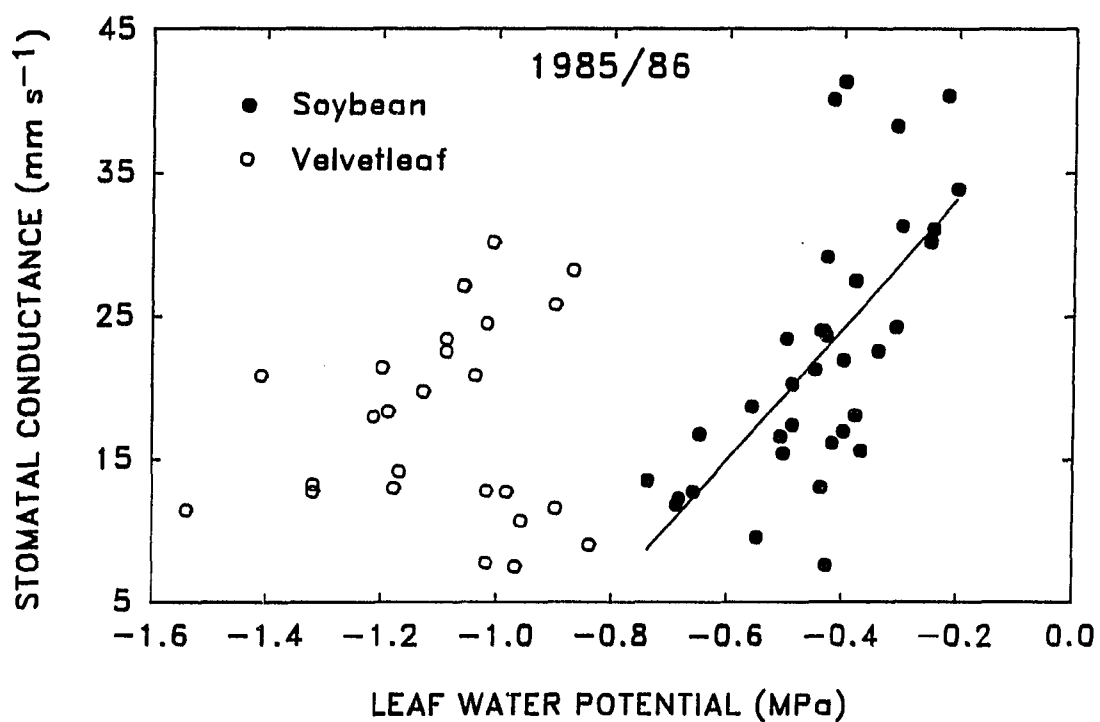


Figure 5. Relationship between midday stomatal conductance and leaf water potential for intercropped velvetleaf and soybean in 1985 and 1986 at Ames, IA. For soybean the regression equation is: $Y = 42.42 + 45.72X$ ($r^2 = 0.44$). No significant relationship was found for velvetleaf.

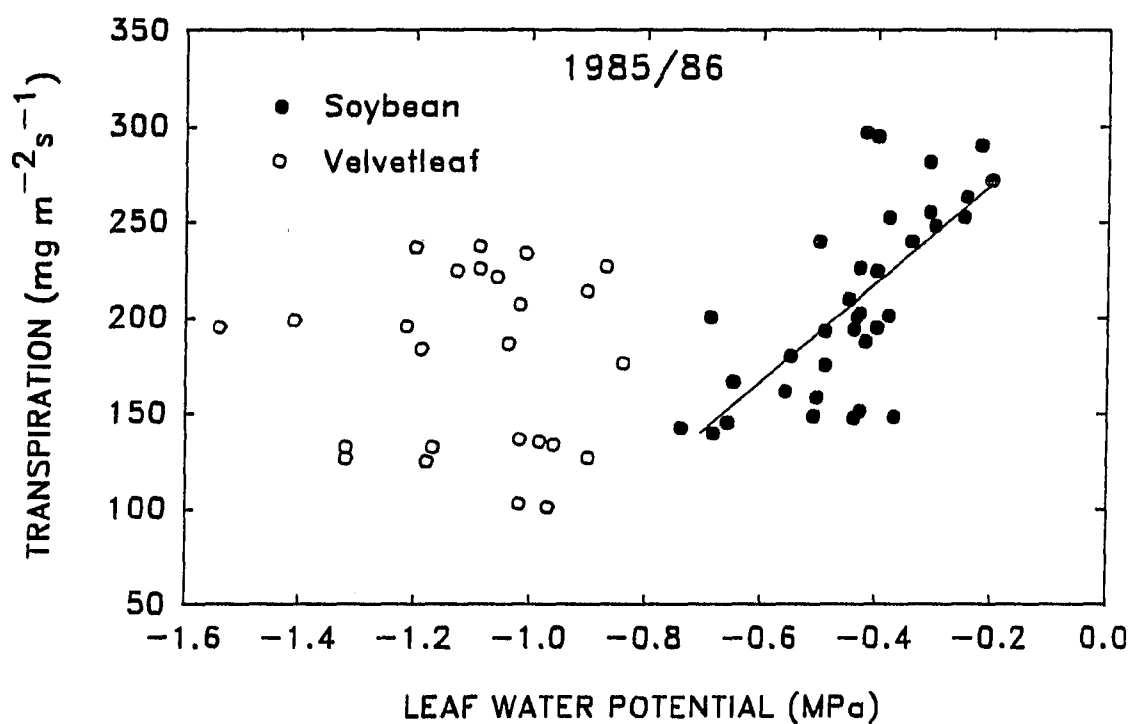


Figure 6. Relationship between midday transpiration rate and leaf water potential for intercropped velvetleaf and soybean in 1985 and 1986 at Ames, IA. For soybean the regression equation is: $Y = 321.73 + 258.54X$ ($r^2 = 0.49$). No significant relationship was found for velvetleaf.

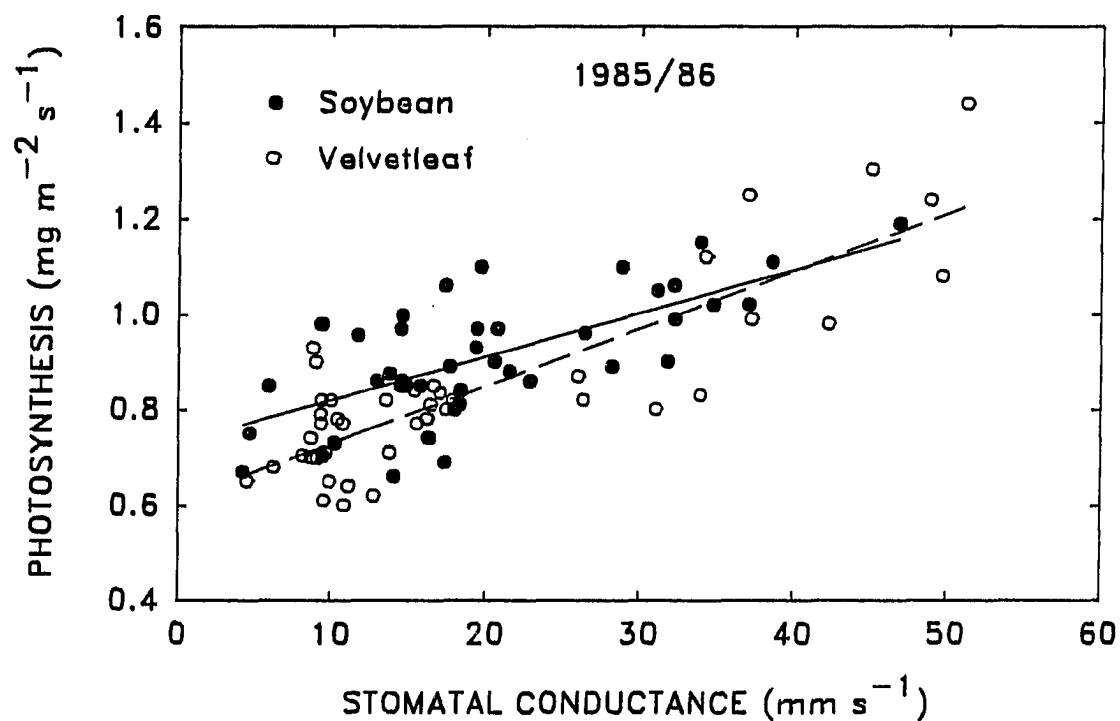


Figure 7. Relationship between net photosynthetic rate and stomatal conductance for intercropped velvetleaf and soybean in 1985 and 1986 at Ames, IA. The regression equations are: $Y = 0.73 + 0.01X$ ($r^2 = 0.46$) for soybean (solid line), and $Y = 0.61 + 0.01X$ ($r^2 = 0.72$) for velvetleaf (dashed line). The regression lines are not significantly different.

SECTION II. GROWTH ANALYSIS OF INTERCROPPED SOYBEAN AND VELVETLEAF

Growth Analysis of Intercropped Soybean (Glycine max)
and Velvetleaf (Abutilon theophrasti)

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ABSTRACT

Growth characteristics of intercropped soybean and velvetleaf plants were compared during 1985 and 1986 in a field study at Ames, Iowa. Soybean plants initially were taller and had more leaf area and total aboveground dry matter than intercropped velvetleaf. However, by midseason there were no interspecific differences in height and velvetleaf had surpassed soybeans in amount of leaf area and total dry weight per plant. By season-end velvetleaf plants had produced 3 to 4 times more aboveground dry matter than soybeans. Early in the season velvetleaf allocated more resources to leaf material and less to stem material in comparison to soybean; however, a reversal of this pattern was observed later in the season. Velvetleaf mean relative growth rates (RGR) and net assimilation rates (NAR) were consistently greater than those of soybean. A rapid rate of growth and an efficient allocation pattern of dry matter appear to contribute to the success of velvetleaf as a weed of soybean. These factors, along with tall stature and an open, branching canopy architecture, appear to allow velvetleaf to successfully compete for irradiance with the soybean crop.

Nomenclature: soybean, Glycine max L. Merr. 'Corsoy 79'; velvetleaf, Abutilon theophrasti Medic.

Additional index words. Competition, dry matter partitioning, relative growth rate, net assimilation rate.

INTRODUCTION

It is well documented that velvetleaf interferes with soybean growth and causes reductions in seed yield (Dekker and Meggitt, 1983; Eaton et al., 1976; Hagood et al., 1980; Higgins et al., 1983 and 1984b; Munger et al., 1987; Oliver 1979). However, the morphological or physiological bases of velvetleaf competitive success in soybean have been little studied. Knowledge of such characteristics could result in more efficacious control and aid in the selection of more competitive crop varieties (Patterson, 1982; Radosevich and Holt, 1984).

Studies comparing the growth and development of crops and associated weeds should lead to a better understanding of weed - crop competition. Relatively few such studies appear in the literature. Field-grown (in containers) soybean and velvetleaf plants showed no differences in RGR, NAR, or specific leaf area (SLA) during vegetative growth (Regnier et al., 1988). However, leaf area ratio (LAR) and leaf weight ratio (LWR) were greater for velvetleaf. After 10 weeks of growth, intercropped velvetleaf were taller and had more main stem nodes and greater dry weight than soybean plants (Munger et al., 1987). The success of common cocklebur (Xanthium strumarium L.) in soybean was attributed to rapid early growth and root elongation rate, while tall morningglory (Ipomoea purpurea (L.) Roth.) was successful due to rapid shoot elongation (Monks et al., 1988).

Several investigators have evaluated weed versus crop growth characteristics under greenhouse or growth chamber conditions. During

early growth, velvetleaf and cotton were judged to be approximately equal in competitive ability, even though cotton was taller and had more leaf and stem dry weight than velvetleaf. Leaf area and total plant dry weight also tended to be greater for cotton (Elmore et al., 1983). In other studies, velvetleaf dry matter production, relative growth rate, relative leaf area expansion rate (LAER), net assimilation rate, leaf area duration (LAD), and leaf area partitioning (LAP) were greater than those of cotton during the first 4 to 6 weeks of growth (Patterson et al., 1978; Patterson and Flint, 1979; Patterson, 1988). Water stress reduced dry matter production, NAR, and LAD less for cotton than for velvetleaf, suggesting that drought conditions during vegetative growth may increase cotton competitiveness relative to velvetleaf (Patterson, 1988).

Under growth chamber conditions, RGR and LAER of 1 to 4 week old velvetleaf were consistently higher than those of soybean, and the interspecific differences were greater under warmer temperatures (Potter and Jones, 1977). In another study, 4 week old velvetleaf plants had less leaf area and less total dry weight than soybeans, and leaf area duration (LAD) and dry matter production were greater for soybean, while velvetleaf had slightly higher net assimilation rates (Patterson and Flint, 1983). In addition, velvetleaf had allocated less dry matter to stem and more to leaf weight and area in comparison to soybean.

In the present study, we monitored aboveground growth characteristics of intercropped soybean and velvetleaf plants in the field throughout the growing season. Our objective was to investigate

the role of plant morphological and growth parameters in velvetleaf competitive success in soybean.

MATERIALS AND METHODS

Field plot establishment. A 2 year field study was conducted on the Curtiss Research Farm at Ames, IA. In 1985 the soil type was Nicollet loam (fine-loamy, mixed, mesic Aquic Hapludolls), and in 1986 the plots were established on Clarion loam (fine-loamy, mixed, mesic Typic Hapludolls). Standard midwestern fertilizer and seeding practices were used to plant soybeans. Treatments consisted of both monocultured soybeans (at 35/m²) and soybeans (at 35/m²) intercropped with velvetleaf at 0.5, 1.0 and 2.0 per m². These weed densities simulate conditions where velvetleaf control methods have been only partially effective. In addition, since the outcome of competition can depend on the environmental conditions under which it occurs (Begon et al., 1986; Fitter and Hay, 1987), an additive design was employed in order to simulate weed - crop interference in a cropping situation. Experimental design was a randomized complete block with 8 replications of each treatment in 1985 and 6 in 1986. Velvetleaf seeds were hand planted approximately 10 cm from the soybean row and were spaced along the row. Soybeans were seeded on May 15 in 1985 and on May 22 in 1986, while velvetleaf were seeded on May 16 in 1985 and May 22 in 1986. Both species were overseeded and then thinned to the desired densities after emergence. Emergence for both species was May 23 in 1985 and May 29 in 1986. Plot size was 6 rows (0.76 m apart) by 9.8 m in 1985 and 10.4 m in 1986. Sethoxydim, 2-[1-(ethoxyimino)butyl]-5-[2-(ethylthio)propyl]-3-hydroxy-2-cyclohexen-1-one, at 0.2 kg ai/ha (1986 only) and hndweeding

were used to control weeds. Rainfall data were gathered from an on-site gauge and from a National Weather Service station 9.6 km to the west.

Growth analysis harvests. For both species biweekly destructive harvests were begun at about 5 weeks after emergence (WAE) at soybean stage V5 (Fehr et al., 1971) in late June and continued through physiological maturity at soybean R8 in September (about 15 WAE). Subsamples consisted of 12 plants per plot for soybean and 2 to 4 plants per plot for velvetleaf. Plants were cut at soil level. Soybean plants were harvested in relation to a velvetleaf plant as follows. At 2 locations per plot, 2 soybean plants were selected from each of 3 positions. Position 1 was adjacent to a velvetleaf plant, position 3 was halfway between 2 weed plants and position 2 was halfway between positions 1 and 3. Parameters recorded for both species included plant height (measured from the first node to the apical meristem), growth stage (for velvetleaf growth stage descriptions see Higgins, 1984a), number of lower leaves abscised, number of branches, and number of branch nodes. Total leaf area was determined with a portable area meter⁴. Plants were separated into leaf, stem (including petiole), and reproductive components and dry weights determined by drying to constant weight at 60 C. The interval method was used to calculate growth analysis parameters (Radford, 1967; Hunt, 1982; Patterson and Flint, 1983). The formulae used are presented in Table 1.

⁴ Model LI-3000, Li-Cor Inc., Lincoln, NE.

Statistical analyses. Analyses of variance were employed for statistical treatment of the data. The monoculture treatment was deleted for the species comparisons, and since subsequent analyses revealed no significant treatment or position effects, the means presented are the averages over the 3 velvetleaf density treatments and the 3 soybean positions sampled. The additive design of the treatments resulted in slight variations in total plant density and the proportion of crop to weed plants over the 3 treatments used for species comparisons. However, since no significant treatment effects were detected for either species, we feel that these variations did not have a significant confounding effect. When the F values were significant (0.05 level) least significant differences (0.05 level) were computed to differentiate among mean values.

RESULTS AND DISCUSSION

Precipitation. The 1985 and 1986 growing seasons differed in rainfall pattern. Precipitation was well below the longterm average in 1985 through midseason, while in 1986 rainfall was above average for every month from April through September (Table 2).

Plant morphology and development. Interspecific differences in plant height, node and branch production, and lower leaf abscission were present during both years of the study. In 1985 soybean plants were significantly taller than intercropped velvetleaf through mid July at 48 days after emergence (Table 3). By early August (75 days after emergence), however, velvetleaf had overtopped the soybean canopy. A similar seasonal pattern was seen in 1986 except that early in the season no significant differences in height were detected. By season end in 1985 velvetleaf averaged 60 cm taller than soybean.

Tall stature is advantageous to a weed as it allows successful competition for photosynthetically active radiation (PAR). Stoller and Woolley (1983) concluded that most of the soybean yield reduction due to velvetleaf interference could be attributed to competition for PAR. Several other studies have indicated that velvetleaf mainly interferes with soybean growth during its reproductive stages when the weed is overtopping the crop (Munger et al., 1987; Oliver, 1979; Hagood et al. 1980). However, there is some evidence that these 2 species may also

compete for water, especially during periods of limited precipitation (Cheetham and Taylor, 1989).

Velvetleaf consistently had more main stem nodes than intercropped soybean (Table 3). The differences were greatest late in the season when velvetleaf was considerably taller than soybean. However, velvetleaf had a greater number of main stem nodes even early in the season when soybean was taller. Lower leaf abscission was also consistently greater for velvetleaf in comparison to soybean so that throughout the growing season velvetleaf had a higher proportion of main stem nodes missing primary leaves. By late August of both years soybean had approximately 40% of main stem nodes missing leaves while for velvetleaf the percentage was 55 to 60%. This could be an adaptation by velvetleaf to concentrate resources close to the canopy top where irradiance is not a limiting factor.

Branch production was greater for soybean through day 48 in 1985 and through day 61 in 1986 (Table 3). Thereafter velvetleaf had greater numbers of branches per plant. Field observations indicated that most of these branches originated from nodes or other branches that were located above or subsequently grew above the soybean canopy. Prolific production of branches above the soybean canopy should also aid velvetleaf in efficient capture of PAR.

Velvetleaf success in soybean may also be aided by a slightly longer period of vegetative growth. Soybean plants were flowering by the second harvest at 46 to 48 days after emergence, while velvetleaf flowered 1 to 2 weeks later. This time difference should have allowed

velvetleaf to produce additional leaf and stem material before resources were directed to reproductive growth.

Plant leaf area and dry matter production. Early in the season soybean plants had more total leaf area per plant than intercropped velvetleaf (Table 4). However, a reversal occurred by late July (about 60 days after emergence), at which time velvetleaf had significantly more leaf area on a plant basis. Thus by midseason velvetleaf plants equalled soybeans in terms of both height and leaf area. At that time soybeans were at the R4 to R5 growth stage - a period during which they become especially vulnerable to stress-induced yield reductions (Shaw and Laing, 1966). In both species leaf areas declined toward season end due to leaf senescence and abscission.

Interspecific differences in plant aboveground dry weight were apparent during both years of the study (Table 4). Although soybean had greater aboveground dry weight early in the season, by 60 days after emergence and beyond, velvetleaf plants had greater aboveground biomass. Late in the season velvetleaf plants had 3 to 4 times the aboveground dry weight of intercropped soybeans. Leaf and stem dry weights showed the same seasonal pattern as total dry weight. Early season leaf and stem weights were greater for soybean but by midseason velvetleaf had greater leaf and stem biomass. The interspecific differences were greatest for stem material. Late season velvetleaf stem dry matter was up to 6 times that of soybean. Capsule dry weight for velvetleaf was

generally greater than pod dry weight of soybean with the differences being greatest late in the season.

Little information is available concerning the characteristics of the velvetleaf root system, although one study reported that R6 stage soybeans extract water from deeper in the soil profile than intercropped velvetleaf (Munger et al., 1987).

Dry matter allocation. Intercropped soybean and velvetleaf differed in seasonal pattern of biomass allocation. Specific leaf weight (SLW) is leaf weight per unit leaf area. It was calculated on a whole plant basis and therefore provides only an indication of average leaf thickness. By 48 days after emergence in 1985 and 61 days after emergence in 1986 velvetleaf SLW was greater than that of soybean and the interspecific differences became greater as the season progressed (Table 5). Leaves of velvetleaf had more prominent veins than soybean leaves (field observation) so this may partly account for the greater SLW of velvetleaf. High SLW could also be a function of velvetleaf height and canopy architecture which may allow greater numbers of sun leaves in comparison to soybean. Sun leaves are generally thicker than shade leaves, and, under conditions of high PAR, usually have higher maximal rates of photosynthesis and increased water use efficiency (Nobel, 1983; Yun and Taylor, 1986).

Soybean and velvetleaf differed in partitioning of dry matter to leaf and stem material. Leaf area ratio (LAR) is the proportion of total aboveground plant dry weight partitioned into leaf material in

terms of area, while leaf weight ratio (LWR) is the same relationship but on a leaf weight basis. Early in the season velvetleaf plants partitioned more dry matter to leaf material in terms of both leaf area and leaf weight (Table 5). However, by 46 to 48 days after emergence LAR was greater for soybean and this remained true for the remainder of the season. Soybean LWR surpassed that of velvetleaf by 61 to 62 days after emergence. Stem weight ratio (SWR) was higher for soybean at 33 days after emergence for both years, but by 61 to 62 days after emergence and beyond velvetleaf had a higher SWR (Table 5). In a greenhouse study, Patterson and Flint (1983) reported that 4 week old velvetleaf had a higher LWR and LAR and a lower SWR than soybean. This agrees with our early season results. Regnier et al. (1988) also found that velvetleaf LWR and LAR were greater than those of soybean during vegetative growth. Leaf to stem ratios (LSR) indicated that velvetleaf had more leaf material per gram stem material early in the season, while soybean had a higher LSR later in the season (Table 5).

Interspecific differences in dry matter partitioning may partially account for velvetleaf competitive success in soybean. Early in the season velvetleaf allocated more resources to leaf production and less to stem material in comparison to soybean. This could allow velvetleaf to achieve a high rate of growth at a time when irradiance is not a limiting factor. Later when the soybean canopy begins to close and competition for PAR becomes critical, velvetleaf allocates more resources to stem material and therefore becomes competitive by growing taller.

Plant growth rates and leaf area duration. Interspecific differences in mean RGR were evident (Table 6). Mean RGR is dry weight gain per unit initial dry weight. Velvetleaf RGR exceeded that of soybean for every time interval in 1985 and through the third interval in 1986. The higher RGR for velvetleaf during the first interval (approximately 33 to 47 days after emergence) is especially interesting in that during this period soybean total leaf area exceeded or equaled that of velvetleaf plants (Table 4). Cheetham and Taylor (1989) reported that early season midday stomatal conductance and net photosynthetic rates were higher for velvetleaf than for intercropped soybean plants. Therefore, rapid growth by velvetleaf during vegetative stages may be at least partially attributed to a higher gaseous exchange capacity.

Mean NAR is the net gain of dry matter per unit leaf area. It usually decreases during the growth and development of a plant stand due to increased competition for PAR and other resources. Velvetleaf NAR was significantly greater than that of soybean with the exception of the third growth period in 1985 (Table 6). Thus velvetleaf produced more aboveground dry matter per unit leaf area than did soybean. In addition, during the 1986 season velvetleaf NAR significantly increased between the first and third intervals. High NAR may be at least partly a function of velvetleaf height and leaf canopy architecture which appear to optimize interception of irradiance. Other investigators have also reported higher RGR and NAR for velvetleaf in comparison to soybean; however, these studies were conducted under controlled

environment conditions and ended after 4 weeks of plant growth (Potter and Jones, 1977; Patterson and Flint, 1983).

No early season differences in mean plant growth rate (PGR) were detected (Table 6). Thus the PGR or dry matter gain per day for velvetleaf plants equalled that of soybeans early in the season even though during at least part of this period velvetleaf plants had less leaf area and aboveground dry weight (Table 4). By the third interval in 1985 and the second in 1986, velvetleaf PGR exceeded that of soybean. Leaf area duration (LAD) is a measure of the amount of leaf area present during a time period. Plant LAD, along with NAR, is important in determining total dry matter production. From mid to late season, velvetleaf LAD tended to be greater than that of soybean but the differences were significant only for the last 2 growth intervals in 1985 (Table 6).

Harper (1977) has stated that good competitors are generally those plants that grow taller and larger sooner than their neighbors. This does not appear to be the case in soybean - velvetleaf competition. Our results indicate that soybeans outgrew velvetleaf early in the season in terms of height, leaf area, and total aboveground dry weight, probably as a result of larger seed size. However, a rapid rate of growth and efficient allocation of dry matter allowed intercropped velvetleaf to become competitive with soybeans by midseason. Efficient production and spatial and temporal arrangement of leaf and stem material appear to allow velvetleaf to successfully compete for irradiance with the soybean crop.

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Table 1. Mathematical growth analysis formulae.

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- A. Calculations for instantaneous values using data from each harvest separately, where A = leaf area (m^2), and W, L, and S = dry weights (g) of total plants and leaf and stem components, respectively.
1. Specific leaf weight (SLW) = L/A , (g m^{-2})
 2. Leaf weight ratio (LWR) = L/W , (g g^{-1})
 3. Leaf area ratio (LAR) = A/W , ($\text{m}^2 \text{g}^{-1}$)
 4. Stem weight ratio (SWR) = S/W , (g g^{-1})
 5. Leaf to stem ratio (LSR) = L/S , (g g^{-1})
- B. Calculations for mean values over the time interval T_1 to T_2 in days, where W_1 and W_2 = plant dry weight (g) at the beginning and end of the interval, respectively, and A_1 and A_2 = total leaf area (m^2) at the beginning and end of the interval, respectively.
1. Plant growth rate (PGR) = $(W_2 - W_1)/(T_2 - T_1)$, (g day^{-1})
 2. Relative growth rate (RGR) =
 $(\ln W_2 - \ln W_1)/(T_2 - T_1) \times 100$, ($\text{g g}^{-1} \text{day}^{-1}$)
 3. Net assimilation rate (NAR) =
 $(W_2 - W_1)(\ln A_2 - \ln A_1)/(T_2 - T_1)(A_2 - A_1)$, ($\text{g m}^{-2} \text{day}^{-1}$)
 4. Leaf area duration (LAD) = $(A_1 + A_2)(T_2 - T_1)/2$, ($\text{m}^2 \text{day}$)
-

Table 2. Monthly precipitation for the 1985 and 1986 growing seasons and the 30 year average precipitation at Ames, Iowa.

Month	Precipitation		
	1985	1986	30 year average
	----- (cm) -----		
April	3.1	13.2	8.6
May	3.2	13.8	11.1
June	6.1	16.9	13.0
July	5.2	11.5	8.8
August	15.8	11.2	9.9
September	10.2	17.5	8.2
Total	43.6	84.1	59.6

Table 3. Plant height, node and branch production, and number of lower leaves abscised of intercropped soybean and velvetleaf in 1985 and 1986 at Ames, Iowa^a.

Days after emergence		Species	Plant height		Main stem nodes		Lower leaf abscission		Branches	
1985	1986		1985	1986	1985	1986	1985	1986	1985	1986
			---(cm)---		----- (no./plant) -----					
33	33	Soybean	18a	23a	5.5b	5.8b	0.2b	0.0b	0.5a	0.3a
		Velvetleaf	12b	21a	6.2a	8.1a	1.0a	1.2a	0.0b	0.0b
48	46	Soybean	47a	59a	8.9b	9.7b	2.3b	2.1b	1.3a	0.9a
		Velvetleaf	44b	57a	12.2a	13.0a	4.8a	5.4a	0.3b	0.0b
62	61	Soybean	78a	114a	11.8b	14.3b	3.7b	5.1b	1.4a	1.8a
		Velvetleaf	80a	113a	17.1a	18.4a	8.1a	8.5a	2.7a	1.0b
75	74	Soybean	99b	129b	13.6b	15.3b	4.3b	5.7b	1.2b	2.3b
		Velvetleaf	112a	150a	19.8a	20.9a	10.1a	9.9a	5.3a	4.7a
89	90	Soybean	102b	135b	13.8b	15.8b	5.2b	6.8b	1.2b	2.4b
		Velvetleaf	147a	157a	22.9a	22.0a	12.5a	13.4a	10.5a	5.5a
101	104	Soybean	98b	--	13.6b	--	6.9b	--	0.7b	--
		Velvetleaf	156a	--	23.6a	--	15.9a	--	13.1a	--

^aMeans within a year and sampling time followed by the same letter are not significantly different, LSD (0.05).

Table 4. Leaf area, total aboveground plant dry weight, and component dry weights of intercropped soybean and velvetleaf in 1985 and 1986 at Ames, Iowa^a.

Days after emergence			Leaf area		Leaf		Stem		Pod/Capsule		Total	
1985	1986	Species	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
			-(m ² /plant)-		------(g/plant)-----							
33	33	Soybean	0.04a	0.04a	1.3a	1.5a	0.8a	1.1a	--	--	2.1a	2.6a
		Velvetleaf	0.01b	0.03b	0.5b	0.9b	0.2b	0.5b	--	--	0.7b	1.4b
48	46	Soybean	0.09a	0.10a	3.1a	3.0a	3.2a	3.6a	--	--	6.3a	6.6a
		Velvetleaf	0.08a	0.09a	3.3a	2.7a	3.3a	3.3a	--	--	6.6a	6.1a
62	61	Soybean	0.11b	0.14b	4.4b	4.6b	5.5b	7.8b	0.4a	0.6b	10.3b	13.0b
		Velvetleaf	0.14a	0.17a	6.2a	7.9a	10.0a	18.2a	0.7a	2.2a	16.8a	28.3a
75	74	Soybean	0.13b	0.13b	5.5b	5.0b	7.6b	9.2b	3.4a	3.4b	16.5b	17.6b
		Velvetleaf	0.21a	0.16a	9.6a	8.5a	21.4a	31.9a	3.7a	10.2a	34.7a	50.5a
89	90	Soybean	0.11b	0.11a	5.0b	4.6b	7.7b	9.2b	8.3b	9.8b	21.0b	23.6b
		Velvetleaf	0.23a	0.12a	12.4a	7.0a	38.7a	33.3a	14.8a	22.9a	65.9a	63.1a
101	104	Soybean	0.07b	0.05a	2.8b	1.6a	6.5b	7.6b	10.8b	12.9b	20.0b	22.0b
		Velvetleaf	0.18a	0.05a	9.8a	2.3a	41.7a	26.2a	29.4a	25.8a	80.9a	54.4a

^aMeans within a year and sampling time followed by the same letter are not significantly different, LSD (0.05).

Table 5. Dry weight allocation of intercropped soybean and velvetleaf in 1985 and 1986
at Ames, Iowa.

Days after emergence			Specific leaf weight		Leaf area ratio		Leaf weight ratio		Stem weight ratio		Leaf to stem ratio	
1985	1986	Species	1985	1986	1985	1986	1985	1986	1985	1986	1985	1986
			---(g/m ²)--		---(m ² /g)---		----- (g/g) -----					
33	33	Soybean	36.6	35.2	0.017	0.017	0.64	0.58	0.36	0.42	1.74	1.38
		Velvetleaf	34.8	35.2	0.020	0.019	0.68	0.66	0.32	0.34	2.64	1.97
48	46	Soybean	34.9	29.8	0.014	0.015	0.49	0.45	0.51	0.55	0.96	0.82
		Velvetleaf	41.1	32.7	0.012	0.014	0.51	0.45	0.49	0.55	1.04	0.82
62	61	Soybean	39.1	33.4	0.011	0.010	0.43	0.35	0.53	0.60	0.80	0.59
		Velvetleaf	43.4	46.3	0.009	0.006	0.37	0.28	0.59	0.65	0.63	0.44
75	74	Soybean	42.0	36.7	0.008	0.008	0.33	0.28	0.46	0.52	0.72	0.54
		Velvetleaf	45.4	53.6	0.006	0.003	0.28	0.17	0.62	0.63	0.45	0.27
89	90	Soybean	44.5	42.0	0.005	0.005	0.24	0.19	0.37	0.39	0.66	0.50
		Velvetleaf	54.6	59.8	0.003	0.002	0.19	0.11	0.59	0.53	0.31	0.21
101	104	Soybean	42.6	34.2	0.003	0.002	0.13	0.07	0.32	0.34	0.41	0.21
		Velvetleaf	54.9	47.1	0.002	0.001	0.11	0.04	0.52	0.48	0.24	0.08
LSD _{0.05}			2.4	6.1	0.001	0.0006	0.02	0.01	0.02	0.02	0.24	0.05

Table 6. Relative and plant growth rates, net assimilation rates and leaf area duration of intercropped soybean and velvetleaf in 1985 and 1986 at Ames, Iowa.

Days after emergence	Species	Relative growth rate		Plant growth rate		Net assimila- tion rate		Leaf area duration	
		1985	1986	1985	1986	1985	1986	1985	1986
		-(g/g/dayx100)-		---(g/day)---		--(g/m ² /day)--		---(m ² day)--	
33 to 47	Soybean	7.43	7.11	0.28	0.31	4.83	4.51	0.95	0.94
	Velvetleaf	16.25	11.28	0.41	0.36	11.36	7.23	0.71	0.71
47 to 62	Soybean	5.18	5.62	0.29	0.36	4.26	4.25	1.02	1.06
	Velvetleaf	10.62	10.62	0.54	0.84	9.93	8.59	0.83	0.88
62 to 75	Soybean	3.44	3.40	0.35	0.40	3.03	3.35	1.45	1.78
	Velvetleaf	6.31	7.39	1.10	1.57	7.02	11.66	1.68	1.94
75 to 89	Soybean	2.57	2.07	0.40	0.36	3.41	2.70	1.60	1.79
	Velvetleaf	5.14	2.99	1.86	1.36	8.97	9.44	2.55	2.15
89 to 103	Soybean	0.68	0.68	0.17	0.19	--	--	1.61	1.85
	Velvetleaf	3.30	0.10	1.86	0.26	--	--	3.18	2.06
LSD _{0.05}		1.18	1.02	0.47	0.33	4.68	2.39	0.31	ns

GENERAL SUMMARY AND CONCLUSIONS

Water relations, gas exchange, and growth characteristics of intercropped soybean and velvetleaf plants were evaluated in 1985 and 1986 a field study at Ames, Iowa. Treatments consisted of monocultured soybeans and soybeans intercropped with velvetleaf at 0.5, 1.0, and 2.0 plants per m². Biweekly growth analysis harvests were taken between 5 and 15 weeks after emergence. Leaf areas were measured and leaf, stem, and reproductive component dry weights were determined. Biweekly physiological measurements were taken between 5 and 13 weeks after emergence. Measurements included predawn and midday leaf water potential, midday stomatal conductance, leaf transpiration rate, and leaf net photosynthetic rate. Experimental design was a randomized complete block with 4 or 6 replications. Analyses of variance and linear regression analyses were employed for statistical treatment of the data. The following paragraphs summarize the major findings and conclusions of this study.

Throughout both growing seasons, velvetleaf predawn and midday leaf water potentials were consistently lower than those of soybean. In addition, velvetleaf had a greater seasonal range of predawn leaf water potentials indicating that it may be more responsive to soil moisture status than soybean. Velvetleaf also had a greater diurnal range of leaf water potentials.

Midday stomatal conductances, midday leaf transpiration rates, and daily mean photosynthetic rates were higher for velvetleaf during the

vegetative growth stage of both species, but thereafter were higher for soybean. Thus, velvetleaf was able to maintain a higher rate of gas exchange than soybean early in the season despite having at the same time significantly lower leaf water potential values. A higher gas exchange capacity early in the season most likely contributes to the rapid growth of velvetleaf during vegetative stages.

Soybean and velvetleaf plants differed in the relationship between gas exchange parameters and leaf water potential. Despite consistently lower leaf water potentials, velvetleaf was able to maintain a seasonal range of stomatal conductances and leaf transpiration rates generally comparable to those of soybean. Thus, lower leaf water potentials do not necessarily indicate that velvetleaf is under more water stress than soybean. In addition, stomatal conductance appeared to be less dependent on leaf water potential for velvetleaf in comparison to soybean. The lower leaf water potentials of velvetleaf would result in a larger gradient between plant and soil water potentials. This may enhance velvetleaf competitiveness in soybean by increasing efficiency of soil water extraction.

No interspecific differences were detected in the relationship between leaf photosynthetic rates and stomatal conductance. This suggests that fieldgrown soybean and velvetleaf do not differ in photosynthetic efficiency.

In 1985, the drier than average year, soybeans intercropped with velvetleaf had slightly lower predawn leaf water potentials in comparison to monocultured soybeans. The data indicate that velvetleaf

can influence soybean water relations and therefore competition for water may occur, especially under conditions of low soil moisture. No differences in midday leaf water potentials, midday stomatal conductance, or photosynthetic rates were detected between monocultured and intercropped soybean for either year.

Soybean plants initially were taller and had more leaf area and total aboveground dry matter than intercropped velvetleaf. However, by midseason there were no interspecific differences in height and velvetleaf had surpassed soybeans in amount of leaf area and total dry weight per plant. By season-end velvetleaf plants had produced 3 to 4 times more aboveground dry matter than soybeans. Velvetleaf stem dry weight was up to 6 times that of soybean. Velvetleaf had a slightly longer vegetative growth period and it appeared to concentrate resources close to the canopy top by abscising a greater percentage of lower leaves in comparison to soybean. In addition, from mid to late season velvetleaf produced greater numbers of branches than soybean.

Interspecific differences in dry matter partitioning may partially account for velvetleaf competitive success in soybean. Early in the season velvetleaf allocated more resources to leaf material and less to stem material in comparison to soybean; however, a reversal of this pattern was observed later in the season. This pattern of resource allocation could contribute to the high rate of velvetleaf growth early in the season when irradiance is not a limiting factor. Later when the soybean canopy begins to close and competition for photosynthetically active radiation becomes critical, velvetleaf allocates more resources

to stem material and therefore becomes competitive by growing taller. In addition, velvetleaf specific leaf weight was greater than that of soybean from midseason on, indicating that velvetleaf leaves are on average thicker than those of soybean.

Velvetleaf relative growth rates and net assimilation rates were consistently greater than those of soybean. Velvetleaf appears to have greater aboveground production of dry matter per unit leaf area than soybean. Conceivably the lower xylem water potentials of velvetleaf together with the capacity to maintain high stomatal conductance may result in a photosynthetic production advantage especially as soil moisture becomes limiting.

A rapid rate of growth and efficient allocation of dry matter appear to contribute to velvetleaf success as a weed of soybean. These factors, along with tall stature and an open, branching canopy architecture, appear to allow velvetleaf to successfully compete for irradiance with the soybean crop.

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APPENDIX. SUPPLEMENTAL DATA TABLES

Table 1. Mean diurnal stomatal conductance of intercropped soybean and velvetleaf during vegetative growth. Readings were taken 39 and 36 days after emergence in 1985 (n = 6) and 1986 (n = 12), respectively.

Hour of day	Species	Stomatal conductance	
		1985	1986
----- (mm/s) -----			
9	Soybean	19.7	32.2
	Velvetleaf	30.1	40.5
11	Soybean	18.8	42.6
	Velvetleaf	29.2	44.6
13	Soybean	13.9	27.6
	Velvetleaf	19.0	41.0
15	Soybean	11.6	35.9
	Velvetleaf	19.8	43.4
17	Soybean	8.1	29.9
	Velvetleaf	19.9	32.4
Standard error of mean		1.5	2.6

Table 2. Midday leaf transpiration rates of intercropped soybean and velvetleaf in 1985 and 1986 at Ames, Iowa.

Days after emergence		Species	Transpiration rate	
			1985	1986
1985	1986		----- (mg/m ² /sec) -----	
38	35	Soybean	143.5	209.3
		Velvetleaf	191.0	225.5
52	49	Soybean	190.1	241.8
		Velvetleaf	185.5	229.2
66	71	Soybean	216.8	259.1
		Velvetleaf	210.5	137.3
84	78	Soybean	161.7	294.2
		Velvetleaf	128.2	207.2
96	92	Soybean	159.7	190.2
		Velvetleaf	129.0	110.6
LSD _{0.05}			25.3	19.3

Table 3. Soybean predawn leaf water potential as influenced by density of intercropped velvetleaf in 1985 at Ames, Iowa.

Days after emergence	Velvetleaf density	Leaf water potential
	(plants/m ²)	(-MPa)
38	0.0	0.10
	1.0	0.11
	2.0	0.09
52	0.0	0.11
	1.0	0.18
	2.0	0.15
66	0.0	0.05
	1.0	0.07
	2.0	0.08
84	0.0	0.06
	1.0	0.08
	2.0	0.07
96	0.0	0.03
	1.0	0.04
	2.0	0.04
LSD _{0.05}		0.03

Table 4. Soybean seed yield as influenced by density of intercropped velvetleaf in 1985 and 1986 at Ames, Iowa.

Velvetleaf density	Seed yield	
	1985	1986
(plants/m ²)	----- (kg/ha) -----	
0.0	2542	3233
0.6	2175	3224
1.0	2126	3291
2.0	2091	3125
LSD _{0.05}	235	

Table 5. Water use efficiency and leaf transpiration and photosynthetic rates of intercropped soybean and velvetleaf at Ames, Iowa in 1985.

Days after emergence	Species	Water use efficiency	Transpiration rate	Photosynthetic rate
		--(mg/g)--	--(mg/m ² /s)--	--(mg/m ² /s)--
60	Soybean	9.2	79.0	0.71
	Velvetleaf	9.8	68.5	0.66
87	Soybean	9.8	101.7	0.97
	Velvetleaf	14.6	64.0	0.92
LSD _{0.05}		1.0	10.1	ns